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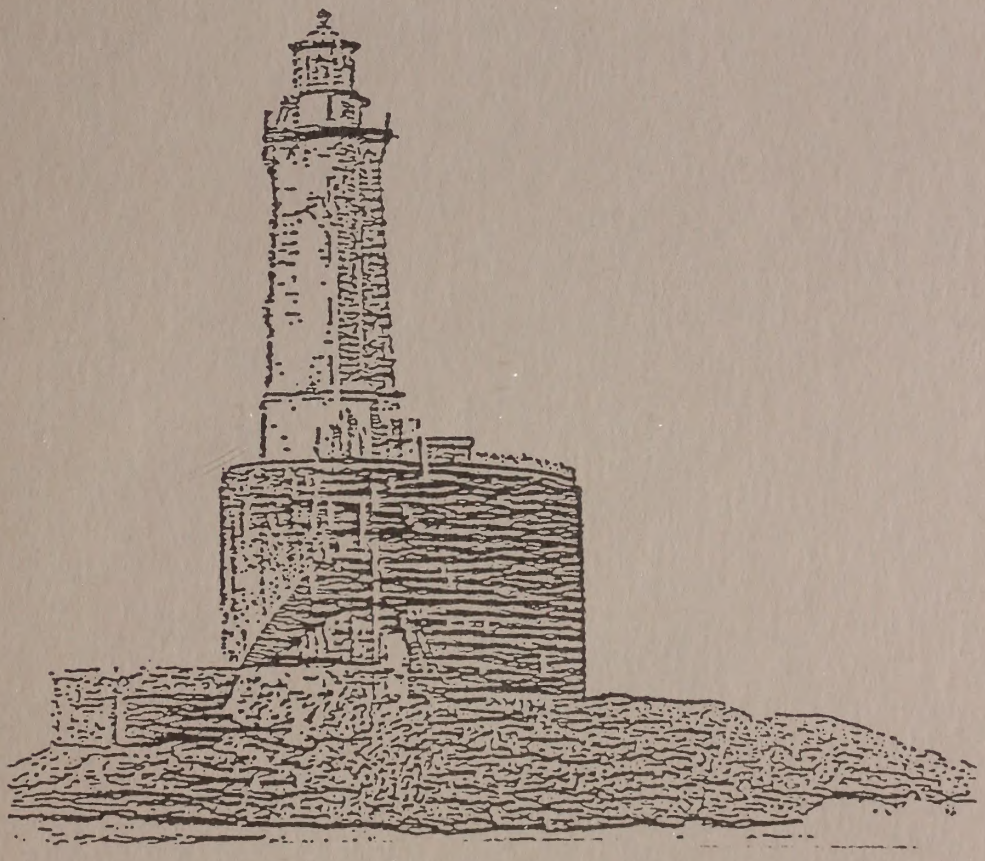

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RECOVERY OF BENTHIC MARINE POPULATIONS ALONG THE PACIFIC COAST OF THE UNITED STATES FOLLOWING NATURAL AND MAN-MADE DISTURBANCES INCLUDING PERTINENT LIFE HISTORY INFORMATION

By

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Intertidal and subtidal benthic communities are not static but frequently change in response to natural (e.g., predation and storms) and man-made (e.g., pollution and experimental clearance) disturbances. Studies conducted along the Pacific coast of California, Oregon, and Washington, indicate that the time needed for benthic marine populations to recover from these disturbances ranges from less than 1 month to over 10 years (Table I). Generally, algal populations recover much more rapidly than invertebrate populations. For a community or association to completely recover, all populations, or at least all of the major populations, must become reestablished at pre-disturbance abundances. This typically requires at least 2 years, and often much longer.

It is difficult to determine the precise time required for a population or community to recover because many factors are influential. Therefore, the recovery times given in Table I should be considered approximations. One very important factor that affects recovery times is the severity of the disturbance. For example, if only the erect thallus of the red alga Endocladia muricata is removed, recovery will occur within 6 months (Glynn, 1965) because the alga can regrow from the holdfast; however, if the holdfast is also destroyed, recovery takes over 27 months (Northcraft, 1948) since new spore colonization is required. Furthermore, the more severe the disturbance in terms of the numbers of species and individuals killed or injured, the total area impacted, and the length of the disturbance, the longer it will take a population to recover.

The year or time of year of a disturbance also may influence how long is needed for community recovery. Extensive repopulation by most species will not begin until their setting period which may be up to a year later for those with short reproductive periods. Additionally, reproductive success varies from year to year and in some cases may not be very successful for several years (Paine, 1974). Once established, a species may enhance or inhibit the recolonization of other species. For example, Paine (1977) reported that when an intertidal area in Washington was cleared in the spring while there were many propagules of the green alga Ulva in the water, Ulva encumbered the spatial resource and prevented or delayed invasion of other species. Therefore, this intertidal area took much longer to regain its mature community structure when it was disturbed in the spring (37 months) than when it was cleared in the autumn (20 months).

The time required for a species or an association to recover also varies from one location to the next. Murray and Littler (1979) reported that recovery was generally slower at the northern end of the Southern California Bight than farther south, probably due to differences in water temperature. Therefore, the information in Table I for a particular taxon or assemblage is roughly arranged with the most northern location first followed by sequentially more southerly located areas.

Another factor affecting recovery time is the amount of disturbance to which a population is normally exposed. For example, Murray and Littler

(1978) reported that an area exposed to sewage pollution took only 0.8 months to recover from experimental clearance by scraping and burning, whereas an unpolluted area took more than 30 months.

Finally, recovery time depends on the abundances of species before the disturbance and in nearby undisturbed areas, and the life histories of the species.

All studies of the time required for Pacific coast benthic marine populations to recover from natural and man-made disturbances of which we are aware have been included in Table I. Typically, recovery has been monitored following the experimental clearance of an area by scraping, burning, or exposing new surfaces by chipping or blasting away with dynamite weathered surfaces. Although these studies are certainly valuable, it is important to recognize that scraping does not completely remove crustose forms, burning may leave chemical residues, and exposing new surfaces by chipping or blasting with dynamite alters the natural rock configuration. Table I also includes 1) recovery studies following contamination by oil, 2) recovery studies following natural disturbances such as predation and storms, and 3) studies concerning the colonization of a new substratum when the time needed for a mature community to become established was indicated.

Recovery times are reported either for an individual species or an entire association. Generally, recovery of an association is much longer than for one species because the former is usually based on the species with the slowest recovery rate. Nearly all of the populations

studied primarily occur on hard surfaces. Most also occur in the intertidal zone.

Recovery times have been determined by a variety of methods (see Table I). Perhaps the most feasible quantitative method for determining recovery of the entire community when controls are available is to compare the percent cover of each species to comparable undisturbed data using a Bray-Curtis similarity coefficient or similar analysis (Cimberg, 1975; Murray and Littler, 1978, 1979). Recovery of a population can be quantitatively determined by comparing percent cover data to pre-disturbance data. In comparing cover values by these methods there is no assurance that the typical size or age class distribution has been reestablished since many small individuals could cover the same area. However, this limitation also exists and is probably more pronounced with other methods, such as those based on presence/absence data (i.e., time when settlement was first observed) and density data. Therefore, although Murray and Littler (1979) reported recovery for macroinvertebrate populations based on density as well as cover, only the recovery times based on cover are included in Table I. In extracting recovery times from the tables presented by Murray and Littler, recovery was considered complete when the percent cover was approximately equal to or greater than the pre-disturbance value. Furthermore, only recovery times of the most abundant species from each of their study areas are shown in Table I because recovery of rare species can be easily affected by a few chance settlements and, therefore, could vary greatly each time it is measured.

Since many populations require a long period to recover, complete recovery was not always observed. Occasionally, the recovery times were estimated. If recovery was not observed or predicted, the time was preceded by a "greater than" sign (>) in Table I to indicate a longer period than observed. A population with a >24 month recovery time may actually recover in 25 months or may require over 10 years. Also, a population with a >12 month recovery time will not necessarily recover faster than one with a >24 month recovery time. Recovery of the first population was merely monitored for a shorter period. A "less than or equal to" sign ($\leq$) signifies recovery occurred by the time indicated, but the last monitoring was not for a long period of time (usually 12 months) so it may have occurred much more rapidly.

Several aspects of the life histories of benthic marine invertebrates greatly influence and can be used to predict recovery times. As noted previously, extensive repopulation by most species will not begin until their setting period which may be up to a year later for those with short reproductive periods. After a new generation has settled, it must reach sexual maturity before it can be assumed that a population will persist in an area. To be completely recovered, a population must reestablish its pre-disturbance size or age class structure which typically includes at least a few individuals near their maximum life expectancies.

Tables II and III provide a summary of information on the life histories of Pacific coast benthic marine invertebrates from rocky and soft bottom

habitats, respectively. In obtaining this information the emphasis was placed on rocky intertidal species, but information on other species was included when obtained. As suggested by Giese and Pearse (1974), spawning season was only used to indicate the period when gametes are released, and was distinguished from the brooding, egg-laying and larval release periods. However, earlier authors often did not distinguish these periods, so determining the proper placement of information was sometimes difficult.

Marine invertebrates spawn during different seasons depending on the species. Those that have been thoroughly studied seem to spawn all year or several times per year rather than in distinct annual cycles. However, reproduction in all species is incompletely known and additional information is needed. For example, even though a species may not have a distinct annual cycle through its entire range, populations or individuals in isolated areas could. This assumption is based on the observation that the spawning season of some species seems to depend on geographic location. Populations in Washington sometimes have spawning seasons which do not overlap at all with populations to the south. Occasionally, spawning may merely start later in more northern areas, perhaps in response to an increase in water temperature to some critical value. Similarly, mating seasons also depend on the species, and part of the variation within a species may be attributable to geographic location. Additionally, spawning or mating seasons may vary during succeeding years.

Since reproduction may vary with geographic location, the life history information provided in Tables II and III has been arranged with the most northern area first. Whenever the location was uncertain, it was listed as "Pacific Coast". These references were probably not the original studies. When information provided by one author for a given area encompasses all of the information from others, the data were pooled on one line and all authors referenced. This is particularly prevalent at Monterey Bay where earlier studies were only conducted during the summer months. However, if the findings conflict, the data are provided on separate lines for each author.

Sexual maturity is reached rapidly, usually by 2 years, for most invertebrates. However, some commercially and ecologically valuable taxa such as the spiny lobster Panulirus interruptus and the red abalone Haliotis rufescens do not reach sexual maturity for about 6 years.

The maximum life expectancy of most invertebrates is about 10 years or less. However, several important species live much longer. For example, the sea anemone Anthopleura elegantissima may live 80+ years, chitons live 20-25+ years, the starfish Pisaster ochraceus lives 34 years, the worm Urechis caupo lives about 25 years, and the pismo clam Tivela stultorum lives from 10 to 53 years.

Several methods have been used to determine spawning times, ages at sexual maturity and maximum life expectancies (see Tables II and III). A description of the methods used to determine spawning times is provided by Giese and Pearse (1974). The value of the methods used to

determine ages at sexual maturity and maximum life expectancies depends on the species and geographic location so the methods sections of the individual publications should be consulted. If a method was not given or was not clear, it was assumed that field observations were used.

In general, interpretation of data was avoided. For example, if the larval period and length were known, the setting period could be surmised. However, unless the author indicated the setting period, it was not given in Tables II or III. Similarly, the setting period of many species probably could be approximated from the raw data of recovery studies listed in Table I. However, this was not done since many types of data can be misinterpreted without a thorough understanding of the study.

Data on the life histories of algae have not been tabulated due to time constraints. Many algae produce spores all year: Sargassum muticum (Nicholson, in press), Gigartina agardhii (West, 1972), Macrocystis pyrifera (Oregon State University, 1971), Gigartina spinosa, Iridaea flaccida, Rhodoglossum affine (Northcraft, 1948), while others reproduce seasonally such as Prionitis lanceolata (Northcraft, 1948). Age at sexual maturity is about 1 year for Macrocystis pyrifera (North, 1971). The life span of some algae is quite short: Egregia menziesii 1 to 2 years (Proctor, 1968), Nereocystis luetkeana 1 to 2 years (Carefoot, 1977; Setchell, 1908), Eisenia arborea 2 years (Foster, 1975). However, articulated coralline algae may live over 10 years (Foster, 1975) and clones of Pterocladia capillacea can persist for at least 40 years

(Dixon, 1973).

In summary, repopulation studies indicate that the time needed for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances ranges from less than 1 month to over 10 years. For a community to completely recover, all populations, or at least all of the major populations, must become reestablished at pre-disturbance abundances. This typically requires at least 2 years, and often much longer. Many factors influence the lengths of these recovery times including the severity of the disturbance, the year or time of year of the disturbance, the geographic location, the amount of disturbance to which a population is normally exposed, the abundances of species before the disturbance and in nearby undisturbed areas, and the life histories of the species. Based on life history information, recovery of most species will begin in less than 1 year, but it cannot be assumed they will persist in an area until sexual maturity is reached. This occurs by 2 years for most species. Complete recovery will not occur until the pre-disturbance size or age class structure is reestablished. Often this requires at least a few individuals near their maximum life expectancies and, therefore, may take 10 years or more. Thus, based both on repopulation and life history information, benthic marine communities will need at least 2 years and often 10 years or more to recover from natural and man-made disturbances. Further recovery and life history studies are necessary to evaluate the effects of these disturbances on marine populations, and to more precisely predict recovery times.

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Table I. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum.

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Macroalgae:					
Chlorophyta (green algae)					
Chaetomorpha linum	Dutch Harbor, San Nicolas Isl., CA[112]	I	Rock	Scraped	3 months[a]
Enteromorpha spp.	Dutch Harbor, San Nicolas Isl., CA[112]	I	Rock	Scraped	9 months[a]
Ulva lobata	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	3 months[a]
	Coal Oil Point, Santa Barbara County, CA[112]				3 months[a]
Ulva taeniata	Government Point Santa Barbara County, CA[112]	I	Rock	Scraped	3 months[a]
Phaeophyta (brown algae)					
Colpomenia sinuosa/peregrina	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	3 months[a]
Egregia menziesii	Whites Point, Los Angeles, CA[112]	I	Rock	Scraped	>24 months[a]
	Cave Canyon, Santa Barbara Isl., CA[112]				12 months[a]
	Fisherman Cove, Santa Catalina Isl., CA[112]				6 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				>24 months[a]
Eisenia arborea	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	≤24 months[a]
Fucus distichus	Portage Head, WA[33]	I	Rock	Virgin rock surfaces exposed by blasting with dynamite or area soaked in a mixture of white gas and diesel oil and burned	≥2-4 years[a]
Halidrys dioica	Willows Anchorage, Santa Cruz Isl., CA[112]	I	Rock	Scraped	>24 months[a]
	Cave Canyon, Santa Barbara Isl., CA[112]				>24 months[a]
	Dutch Harbor San Nicolas Isl., CA[112]				>24 months[a]
	Fisherman Cove Santa Catalina Isl., CA[112]				≤24 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				≤24 months[a]

Table 1. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Phaeophyta (continued)					
Hedophyllum sessile	Waadah Isl., WA[124]	I	Rock	Algal cover scraped off then rock surface sterilized by burning	20 months if cleared in the autumn[a]; 37 months if cleared in the spring[a]
Hesperophycus harveyanus	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Laminaria sinclarii	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	12 months[a]
Macrocystis pyrifera	Santa Cruz Isl., CA[48]	S	New concrete construction blocks	--	1 year[f]
Macrocytis pyrifera algal association	Santa Cruz Isl, CA[48]	S	New concrete construction blocks	--	5-10 years[f]
Pelvetia fastigiata	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
Pelvetia fastigiata f. gracilis	Cuyler Harbor, San Miguel Isl., CA[112]	I	Rock	Scraped	>24 months[a]
	Willows Anchorage Santa Cruz Isl., CA[112]				>24 months[a]
	Fisherman Cove, Santa Catalina Isl., CA[112]				>24 months[a]
Pseudolithoderma nigra	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	3 months[a]
Ralfsiaceae	Whites Point, Los Angeles, CA[112]	I	Rock	Scraped	3 months[a]
	Dutch Harbor, San Nicolas Isl., CA[112]				3 months[a]
Sargassum agardhianum	Wilson Cove, San Clemente Isl., CA[112]	I	Rock	Scraped	>12 months[a]
Rhodophyta (red algae)					
Bossiella orbigniana ssp. dichotoma	Cave Canyon, Santa Barbara Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Ceramium eatonianum/sinicola	Whites Point, Los Angeles, CA[112]	I	Rock	Scraped	3 months[a]
Ceramium spp./ Centroceras clavulatum	Dutch Harbor, San Nicolas Isl., CA[112]	I	Rock	Scraped	3 months[a]

Table 1. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Rhodophyta (continued)					
Corallina officinalis var. chilensis	Willows Anchorage Santa Cruz Isl., CA[112]	I	Rock	Scraped	12 months[a]
	Whites Point, Los Angeles, CA[112]				3 months[a]
	Cave Canyon Santa Barbara Isl., CA[112]				3 months[a]
	Fisherman Cove, Santa Catalina Isl., CA[112]				3 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				3 months[a]
	Ocean Beach, San Diego County, CA[112]				3 months[a]
Corallina vancouveriensis	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
	Coal Oil Point, Santa Barbara County, CA[112]				3 months[a]
	Cuyler Harbor, San Miguel Isl., CA[112]				>24 months[a]
	South Point, Santa Rosa Isl., CA[112]				9 months[a]
	Whites Point, Los Angeles, CA[112]				12 months[a]
	Cave Canyon, Santa Barbara Isl., CA[112]				12 months[a]
	Dutch Harbor, San Nicolas Isl., CA[112]				12 months[a]
	Ocean Beach, San Diego County, CA[112]				12 months[a]
Crustose Corallinaceae	Cuyler Harbor, San Miguel Isl., CA[112]	I	Rock	Scraped	>24 months[a]
	Willows Anchorage, Santa Cruz Isl., CA[112]				12 months[a]
	Cave Canyon Santa Barbara Isl., CA[112]				>24 months[a]
	Fisherman Cove, Santa Catalina Isl., CA[112]				<24 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				9 months[a]
	Ocean Beach, San Diego County, CA[112]				12 months[a]
Cryptopleura corallinara	Whites Point, Los Angeles, CA[112]	I	Rock	Scraped	>24 months[a]
Cryptopleura crispa	Cave Canyon, Santa Barbara Isl., CA[112]	I	Rock	Scraped	>24 months[a]
	Ocean Beach, San Diego County, CA[112]				9 months[a]
Cryptopleura violacea	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]

Table I. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Rhodophyta (continued)					
Endocladia muricata	Monterey Bay, CA[64]	I	Rock	Cropped thallus leaving holdfast	≥6 months[e]
	Monterey Peninsula, CA[118]			Scraped then chipped with sledge hammer until fresh surface uncovered	>27 months[h]
	South Point, Santa Rosa Isl., CA[112]			Scraped	>12 months[a]
	Willows Anchorage, Santa Cruz Isl., CA[112]			Scraped	>24 months[a]
Castroclonium coulteri	Covernment Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
Celidium coulteri/pusillum	Willows Anchorage, Santa Cruz Isl., CA[112]	I	Rock	Scraped	6 months[a]
	Fisherman Cove, Santa Catalina Isl., CA[112]				6 months[a]
Gelidium purpurascens/ robustum	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Cigartina canaliculata	Covernment Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
	Coal Oil Point, Santa Barbara County, CA[112]				12 months[a]
	Cuyler Harbor, San Miguel Isl., CA[112]				9 months[a]
	South Point, Santa Rosa Isl., CA[112]				9 months[a]
	Whites Point, Los Angeles, CA[112]				6 months[a]
	Cave Canyon, Santa Barbara Isl., CA[112]				>24 months[a]
	Dutch Harbor, San Nicolas Isl., CA[112]				3 months[a]
	Fisherman Cove, Santa Catalina Isl., CA[112]				6 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				12 months[a]
Gigartina leptorhyncos	Whites Point, Los Angeles, CA[112]	I	Rock	Scraped	3 months[a]
Cigartina papillata	Monterey Peninsula, CA[118]	I	Rock	Scraped then chipped with sledge hammer until fresh surface uncovered	>1 year[h]
Cigartina spinosa	Monterey Peninsula, CA[118]	I	Rock	Scraped then chipped with sledge hammer until fresh surface uncovered	>6 months[h]
	Cave Canyon, Santa Barbara Isl., CA[112]			Scraped	>24 months[a]

Table I. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Rhodophyta (continued)					
Iridaea flaccida	Monterey Peninsula, CA[118]	I	Rock	Scraped then chipped with sledge hammer until fresh surface uncovered	>3-4 months[h]
Laurencia sinicola	Willows Anchorage, Santa Cruz Isl., CA[112]	I	Rock	Scraped	12 months[a]
Lithothrix aspergillum	Whites Point, Los Angeles, CA[112]	I	Rock	Scraped	>24 months[a]
Petrocelis middendorfii	Cuyler Harbor, San Miguel Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Peyssonneliaceae/ Hildenbrandiaceae	South Point, Santa Rosa Isl., CA[112]	I	Rock	Scraped	3 months[a]
Plocamium cartilagineum	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	3 months[a]
Porphyra perforata	Dutch Harbor, San Nicolas Isl., CA[112]	I	Rock	Scraped	6 months[a]
Prionitis lanceolata	Cuyler Harbor, San Miguel Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Pterocladia capillacea	Fisherman Cove, Santa Catalina Isl., CA[112] Wilson Cove, San Clemente Isl., CA[112]	I	Rock	Scraped	3 months[a] 12 months[a]
Rhodoglossum affine	Monterey Peninsula, CA[118]	I	Rock	Scraped then chipped with sledge hammer until fresh surface uncovered	>3-4 months[h]
Rhodomela larix	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
Rhodophycean turf (assemblage of small red algae)	Coal Oil Point, Santa Barbara County, CA[112]	I	Rock	Scraped	6 months[a]
Smithora naiadum	Government Point, Santa Barbara County, CA[112] Dutch Harbor, San Nicolas Isl., CA[112]	I	Rock	Scraped	>12 months[a] >24 months[a]
Plants:					
Spermatophytina (seed plants)					
Phyllospadix scouleri	South Point, Santa Rosa Isl., CA[112] Dutch Harbor, San Nicolas Isl., CA[112]	I	Rock	Scraped	>12 months[a] ≤24 months[a]

Table I. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Spermatophytina (continued)					
Phyllospadix torreyi	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
	Coal Oil Point Santa Barbara County, CA[112]				12 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				>24 months[a]
	Ocean Beach, San Diego County, CA[112]				12 months[a]
Macroinvertebrates:					
Cnidaria					
Anthozoa (corals, sea anemones)					
Anthopleura elegantissima	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
	Coal Oil Point, Santa Barbara County, CA[112]				>24 months[a]
	Willows Anchorage, Santa Cruz Isl., CA[112]				<24 months[a]
	Dutch Harbor, San Nicolas Isl., CA[112]				>24 months[a]
Annelida					
Polychaeta (segmented worms)					
Dodecaceria fewkesi	Cuyler Harbor, San Miguel Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Phragmatopoma californica	Cuyler Harbor, San Miguel Isl., CA[112]	I	Rock	Scraped	9 months[a]
	South Point, Santa Rosa Isl., CA[112]				9 months[a]
	Dutch Harbor, San Nicolas Isl., CA[112]				6 months[a]
Arthropoda					
Crustacea (lobsters, crabs, shrimps, barnacles)					
Balanus glandula	Goleta Point, near Santa Barbara, CA[144]	I	Rock	Contaminated by crude oil due to Platform A blowout	>16 months on exposed surfaces[h]; >2 months on sheltered surfaces[h]
	South Point, Santa Rosa Isl., CA[112]			Scraped	>12 months[a]

Table I. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Arthropoda - Crustacea (continued)					
Balanus glandula association	Near Trinidad, Humboldt County, CA[21]	I	Rock	Cleared with hammer, chisel and metal brushes	4.8 years[b]
Balanus improvisus	Fruitvald Avenue Bridge, on Oakland Estuary, San Francisco Bay, CA[68]	S	New wooden panels	--	≥2.5 months[d]
Chthamalus dalli association	Near Trinidad, Humboldt County, CA[21]	I	Rock which is periodically buried by sand	Cleared with hammer, chisel and metal brushes	2 months[j]
Chthamalus fissus	Goleta Point, near Santa Barbara, CA[144]	I	Rock	Contaminated by crude oil due to Platform A blowout	>4-6 months[h]
Chthamalus fissus/dalli	Government Point, Santa Barbara County, CA[112]	I	Rock	Scraped	>12 months[a]
	Cuyler Harbor, San Miguel Isl., CA[112]				3 months[a]
	South Point, Santa Rosa Isl., CA[112]				>12 months[a]
	Willows Anchorage, Santa Cruz Isl., CA[112]				>24 months[a]
	Cave Canyon Santa Barbara Isl., CA[112]				>24 months[a]
	Dutch Harbor, San Nicolas Isl., CA[112]				>24 months[a]
	Fisherman Cove Santa Catalina Isl., CA[112]				>24 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				>24 months[a]
	Ocean Beach San Diego County, CA[112]				>24 months[a]
Pachygrapsus crassipes	Duxbury Reef, N. of San Francisco, CA[16]	I	Rock	Contaminated by Bunker C oil from tanker spill	>3 years[c]
Tetraclita squamosa rubescens	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	>24 months[a]
	Wilson Cove, San Clemente Isl., CA[112]				3 months[a]
Mollusca					
Gastropoda (snails, limpets, abalones)					
Collisella digitalis association	Near Trinidad, Humboldt County, CA[21]	I	Rock	Cleared with hammer, chisel and metal brushes	<3.25 years[j]
Dendropoma spp. Petaloconchus montereyensis	Fisherman Cove, Santa Catalina Isl., CA[112]	I	Rock	Scraped	>24 months[a]

Table I. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Mollusca - Gastropoda (continued)					
Littorina planaxis	Duxbury Reef, N. of San Francisco, CA[16]	I	Rock	Contaminated by Bunker C oil from tanker spill	>3 years[c]
Moliusca					
Bivalvia (oysters, clams, mussels)					
Chama arcana	Cave Canyon, Santa Barbara Isl., CA[112]	I	Rock	Scraped	>24 months[a]
Mytilus californianus	Portage Head, WA[33]	I	Rock	Virgin rock surfaces exposed by blasting with dynamite or area soaked in a mixture of white gas and diesel oil and burned	"Many years"[a]
	Oregon (cliff facing NNE)[14]			"Cleared" probably by scraping	>5-6 years[j]
	Oregon (cliff facing SW)[14]			"Cleared" probably by scraping	>8 years[j]
	Duxbury Reef, N. of San Francisco, CA[18]			"Cleaned off" probably by scraping	≥10 years[j]
	Monterey Bay, CA[82]			Scraped then brushed with a steel brush	>2.5 years[j]
	Cuyler Harbor, San Miguel Isl., CA[112]			Scraped	>24 months[a]
	South Point, Santa Rosa Isl., CA[112]			Scraped	>12 months[a]
	Willows Anchorage, Santa Cruz Isl., CA[112]			Scraped	>24 months[a]
	Whites Point Los Angeles, CA[112]			Scraped	>24 months[a]
	Corona del Mar, CA[98]			Predation by the starfish Pisaster ochraceus	≥5-10 years[j]
	Ocean Beach, San Diego County, CA[112]			Scraped	>24 months[a]
	La Jolla, CA[23]			Completely cleared by storms	>4 years[h]
Mytilus californianus - Balanus cariosus association	Near Trinidad, Humboldt County, CA[21]	I	Rock	Cleared with hammer, chisel and metal brushes	9.3 years[b]

Table 1. Time required for benthic marine populations along the Pacific coast of the United States to recover from natural and man-made disturbances or to become established on a new substratum (continued).

Taxon or Association	Geographic Location	Intertidal (I) or Subtidal (S)	Substratum	Type of Disturbance (if any)	Recovery Time
Mollusca - Bivalvia (continued)					
Mytilus edulis	Fruitvald Avenue Bridge on Oakland Estuary, San Francisco Bay, CA[68]	S	New wooden panels	--	>5 months[d]
	Alamitos Bay, Long Beach, CA[129]		Boat dock floats	Scraped	2-7 months[h]
Mytilus edulis-Ulva lobata association	Alamitos Bay marina, Long Beach, CA[128]	S	New float	--	<1 year[j]
Echinodermata					
Echinodea (sand dollars, sea urchins)					
Strongylocentrotus purpuratus	Willows Anchorage, Santa Cruz Isl., CA[112]	I	Rock	Scraped	≤24 months[a]
Miscellaneous Associations					
Odonthalia and Iridaea-Hedophyllum-Lithothamnion association	Oregon[14]	I	Rock	Cleared probably by scraping	2 years[j]
Combination of 18 species	Duxbury Reef, N. of San Francisco, CA[17]	I	Rock	Contaminated by Bunker C oil from tanker spill	>5 years[c]
"Luxurious fouling growth" (invertebrates)	Monterey Harbor, CA[70]	I & S	New creosoted wooden piles	--	5-10 years[j]
Sandy beach assemblage	Cat Harbor, Santa Catalina Isl., CA[145]	I	Sandy beach	Contaminated by wet sticky tar	≥2 years[l]
Gigartina canaliculata/ Corallina officinalis var. chilensis association (unpolluted area)	Wilson Cove, San Clemente Isl., CA[111]	I	Rock	Scraped, wire brushed, scrubbed, then burned with propane torch	>30 months[b,g]
Blue-green algae/Ulva californica association (polluted area)	Wilson Cove San Clemente Isl., CA[111]	I	Rock	Scraped, wire brushed, scrubbed, then burned with propane torch	0.8 months[b,g]
"Plant and animal" association	110 miles south of U.S. border in Baja California[107]	I & S	Rock	Contaminated by dark diesel fuel due to grounding of the Tampico-Maru	3-4 years 90% of species restored but some species still not recovered at 12 years[i]

LEGEND

Criteria used to determine recovery times:

a = percent cover data
b = Bray-Curtis similarity coefficient using percent cover data
c = density data
d = size data
e = dry weight biomass data
f = growth rate and total length
g = diversity
h = time until initial or sizable settlement
i = distribution or abundance of species
j = general field observations

Numbers identify the references

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata.

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Cnidaria Hydrozoa (hydroids, hydrocorals, siphonophores)											
Allopora californica	Central California[121]	S	Males: June-July[b]				Oct-Dec				
Obelia longissima	Pacific Coast[99,130]	S						Summer		<1 month[c]	
	Elkhorn Slough, Monterey County, CA[97]						Aug & Jan				
Cnidaria Anthozoa (corals, sea anemones)											
Anthopleura elegantissima	Pacific Coast[130]	I									80+ years[i]
	Central California[72]		(Asexual reproduction by fission is particularly prevalent from Jan-Mar)								
	San Francisco area, CA[47]		Sept[a]								
Anthopleura xanthogrammica	Elkhorn Slough, Monterey County, CA[97]	I	(Reproduces during the summer months)								
Arthropoda Crustacea (lobsters, crabs, shrimps, barnacles)											
Balanus aquila	Monterey Harbor, CA[70]	I & S							Jan-Mar+		
Balanus cariosus	San Juan Isl., WA[30]	I					Spring				
	Near Trinidad, Humboldt County, CA[21]								Apr+		
Balanus crenatus	Humboldt Bay, CA[94]	I & S							All year (Peak late summer to to early fall)		
	San Francisco Bay Slough, CA[80]		(Breeding season Mar-Nov)								
	Monterey Bay, CA[139]										9 months[f]

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Arthropoda - Crustacea (continued)											
Balanus crenatus (continued)	Monterey Harbor, CA[70]						Apr+		All year	≥18 months[c]	
Balanus glandula	Vancouver Isl., Canada[3]	I		Dec-Jul (Peak Dec-Jan	Jan-May (Peak Feb) & Aug-Sept Length: 2 months		Mar-May (Peak Mar-Apr) & Aug-Sept	Length: 1 month	Spring		
	San Juan Isl., WA[30]						Summer & autumn		May-Oct (Peak May-Aug)	1 year[f]	2 years with predators; ≥10 years without predators[f]
	Near Trinidad, Humboldt County, CA[21]								(Peak May & Dec)		
	San Francisco Bay Slough, CA[80]		(Breeding season discontinued after June)								
	Monterey Bay, CA[64]								Large part of the year (Peak fall and winter)		
	Monterey Bay, CA[70,139]										≥1 year[f]
	Morro Bay, CA[88]				Dec-May & fall Length: 1 month					6 months[c]	
	Santa Barbara, CA[30]								Jan-June		
	Santa Barbara, CA[144]				Jan-June		Jan-Feb & Apr-May		Jan-Mar+		
	La Jolla, CA[3]			Oct-Mar (Peak Oct-Dec	Oct-May (Peak Dec)		(Peak Jan)				
Balanus improvisus	Oakland, CA[68]	I & S							Mar-Oct (Peak Apr & Sept)		

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Arthropoda - Crustacea (continued)											
Balanus tintinnabulum californicus	Monterey Bay, CA[139]	I & S									16 months[f]
	Elkhorn Slough, Monterey County, CA[97]			Spring & summer							
	Southern California[97]			Dec-Jan							
	La Jolla, CA[26,28]				All year		Most of the year	Most of the year (Peak June)	Feb-Dec (Peak June-July)	≤3 months[c]	
Cancer antennarius	Pacific Coast[55,130]	I			Nov-Jan						
	Humboldt Bay, CA[94]			Aug[+]							
	Elkhorn Slough, Monterey County, CA[97]				Dec						
Cancer anthonyi	Elkhorn Slough, Monterey County, CA[97]	I & S		June							
	San Diego, CA[2]										180-252 days[i]
Cancer productus	Humboldt Bay, CA[94]	I & S		Aug[+]							
	Elkhorn Slough, Monterey County, CA[97]			July-Aug							
Chthamalus dalli	Near Trinidad, Humboldt County, CA[21]	I							All year		
	Monterey Bay, CA[139]										≥6 months[f]
	Monterey Bay, CA[70]								Dec[+]		
	Monterey Bay, CA[64]								Late summer to early fall		
Chthamalus fissus	Monterey Bay, CA[64]	I					Sept-Mar[+]				
	Morro Bay, CA[88]				All year (Peak June-Sept) Length: 2 weeks					2 months[c]	
	Santa Barbara, CA[144]				All year				(Peak May-Sept)		
	Santa Catalina Isl., CA[143,144]								Feb-June (Peak June)		

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Arthropoda - Crustacea (continued)											
Hemigrapsus nudus	Puget Sound, WA[130]	I			Early summer						
	Monterey, CA[12,130]				Oct-May						
Hemigrapsus oregonensis	Monterey Bay, CA[84]	I			May+						
Ligia occidentalis	Monterey Bay, CA[84]	I			May-June+						
Pachycheles pubescens	Central Oregon[67]	I			May-June+						
Pachycheles rudis	Central Oregon[67]	I			May-June+						
	Elkhorn Slough, Monterey County, CA[97]				Aug						
	Ocean Beach, San Diego County, CA[97]				Mar-Aug						
	Ensenada, Baja California[97]				Dec						
Pachygrapsus crassipes	Pacific Coast[85]	I			Apr-Sept (Peak Aug)					≤1 year[c,i]	
	Monterey Bay, CA[12,64,84]				Mar-Aug						
Pagurus granosimanus	Monterey Bay, CA[84]	I			Feb, Apr-May+						
Pagurus hirsutiusculus	Elkhorn Slough, Monterey County, CA[97]	I			July+		July-Aug				
Pagurus samuelis	Monterey Bay, CA[84]	I			Feb, Apr-May						
	Monterey Bay, CA[97]				Aug+		Mar+				
	Monterey Bay, CA[75]			Late winter	(Peak spring)			Length: 1 month			3-4 years[c]
	Southern California[75]				Jan-Oct						
Panulirus interruptus	Pacific Coast[99]	I & S			<70 days						
	California[55,81,154]			Jan-Apr	May-June Length: 10 weeks			Length: ≤2 years		≥6 years[c]	>10-11 years[c]
	California[137]				(Peak June)		Mar-Aug	Length: 7-8 months			
	California[34]			Mar-July	Length: 3 weeks			Length: >3-6 months			

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Arthropoda - Crustacea (continued)											
Panulirus interruptus (continued)	San Clemente Isl., CA[108]				May-Aug (Peak June)						>10-11 years[c]
	San Diego, CA[135]							May-Sept[+]			
	Southern California and Baja California[92]							June-Dec (Peak July-Oct) Length: 7.75 months			
Petrolisthes cinctipes	Pacific Coast[130]	I			Mar, May-June						
	Central Oregon[67]				May-June[+]						
	Elkhorn Slough, Monterey County, CA[97]				Jan-June						
	Monterey Bay, CA[12,84]				All year						
Petrolisthes eriomerus	Central Oregon[67]	I			May-June[+]						
Pollicipes polymerus	Monterey Bay, CA[86,91]	I			May-Dec Length: 30 days					>6 months[c]	
	Santa Barbara, CA[144]				All year (Peak Feb)						
	Point Dume, Near Santa Monica, CA[4]									5 years[f]	20 years[f]
Pugettia producta	Elkhorn Slough, Monterey County, CA[97]	I & S			Feb, Mar, July						
	Monterey Bay, CA[12,84]				All year						
Tetraclita squamosa rubescens	Monterey Harbor, CA[70]	I							July-Dec		
	Morro Bay, CA[88]				June-Sept Length: 1.5 months					2 years[c]	
Mollusca Polyplacophora (chitons)											
Cryptochiton stelleri	Friday Harbor, WA[100]	I & S									25[+] years[g]
	Oregon[125]		June-July[c]								20 years[c]
	California[78]		(Breeds Feb-Mar)							2 years[c]	
	Monterey Bay, CA[147]		Mar-May[+c]								

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Polyplacophora (continued)											
Katharina tunicata	Central California[62,99]	I	Mar-July (Peak July)[a,c]								
	Monterey Bay, CA[84]		May[d]					July+			
	Monterey Bay, CA[78]									2 years[c]	
Mopalia hindsii	Monterey Harbor, CA[62]	I & S	Feb-Mar & Nov-Dec+[a]								
Mopalia lignosa	Central California[149]	I & S						Length: 5-7 days			
Mopalia muscosa	Puget Sound, WA[99]	I	July-Aug[c]								
	Central California[149]							Length: 11-12 days			
	Monterey Bay, CA[84]		Sept[d]								
	Santa Monica Bay, CA[10,109]		Winter-spring[a,b]								
	Corona del Mar, Orange County, CA[99]		Nov[c]								
Nuttallina californica	Pacific Coast[99]	I									20-25 years[c]
Stenopiax heathiana	Pacific Coast[99]	I						Length: <1 day			
	Monterey, CA[76,84]		May-June[c,d]								
Tonicella lineata	Vancouver, Canada[87]	I & S	Apr+[c]								
	Oregon[5]							Length: 1 week			
Mollusca Gastropoda (snails, limpets, abalones)											
Acanthina punctulata	Monterey Bay, CA[84]	I				May-June					
Acanthina spirata	Elkhorn Slough, Monterey County, CA[97]	I				July					
Acmaea mitra	Central California[56]	I & S	Dec-Mar[b]								
Aplysia californica	Pacific Coast[130]	I & S				All year					
	California[96]					Oct-Mar					
	Elkhorn Slough, Monterey County, CA[97,99]			July, Aug, Nov+		Nov+				2 years[c]	2 years[c]

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Gastropoda (continued)											
Collisella asmi	Central California[59]	I	Mar-Apr & Sept-Oct[b,e]								
Collisella digitalis	Coos Bay, OR[49]	I									6 years[f]
	Rockaway Beach, San Mateo County, CA[58]		Jan-May[b]								
	Moss Beach, San Mateo County, CA[58]		Apr, June-July, Dec[b]								
Collisella limatula	Central California[58]	I	Sept-Oct[b]								
	Monterey Bay, CA[84]		Sept[+d]								
	Palos Verdes, CA[133,134]		Apr-Jan (Peak Sept-Oct)[c]								2.75 years[f,h]
Collisella pelta	Rockaway Beach, San Mateo County, CA[58]	I	Fall, winter spring[b]								
Collisella scabra	Bodega Bay, Sonoma County, CA[146]	I	Jan-Mar & fall[c]						All year (Peak July-Oct)		7-11 years[f,h]
	Rockaway Beach, San Mateo County, CA[59]		3 times 1) late winter -early spring 2) early summer 3) late fall[b]								
	Monterey Bay, CA[84]		Sept[+d]								
	Monterey Bay, CA[74]								(Peak summer & early fall)		
Collisella strigatella	Coos Bay, OR[49]	I									4 years[f,c]
	Santa Barbara, CA[144]		Apr[+c]								
Haliotis cracherodii	Monterey Bay, CA[84]	I & S	Feb-Mar[+c]								
	Monterey Bay, CA[11,150]		June-Oct[a,b]								
	Southern California[95]		Late spring, summer, early fall[a]								
	Palos Verdes, CA[32]		Spring-early summer[+c]								

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Gastropoda (continued)											
Haliotis rufescens	California[55,154]	I & S						Length: 1-2 weeks			
	Near Mendocino, CA[63]		Spring-early summer[b]								
	Central California[32]		Late spring-early fall (Peak late spring-early summer)[c]					Length: 1-2 weeks			
	Monterey, CA[9,79,130,132]		Feb-Apr[c]							6 years[c]	
	Monterey Bay, CA[11]		All year[a]								
Littorina planaxis	Central California[130]	I		Most of the year (Peak spring & summer)							
	Monterey Bay, CA[84]			Mar[+]		Apr[+]		May[+]			
	Monterey Bay, CA[113]			Apr-May							
Littorina scutulata	Monterey, CA[64]	I							Jan-May[+]		
Lottia gigantea	Pacific Coast[99]	I									10-15 years[f]
	Monterey Bay, CA[44]		Mid winter[c]								
Mitra idae	Southern California[15]	I & S				July-Aug					
	La Jolla & Pt. Loma, San Diego, CA[19]			Feb[+]		May-July					
Notoacmea fenestrata	Rockaway Beach, San Mateo County, CA[57]	I	3 times 1) Nov-Dec 2) Jan 3) Mar[b]								
Notoacmea insessa	Moss Beach, San Mateo County, CA[57]	I	4-5 times per year[b]								
	Monterey Bay, CA[127]		Summer[c]					Length: 4 days	Summer & spring (Peak June & Aug-Sept)	<1 year[c,h]	1 year[c,h]
Notoacmea paleacea	Rockaway Beach, San Mateo County, CA[57]	I	Apparently several times per year[b]								

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Gastropoda (continued)											
Notoacmea persona	Oregon[93]	I									6+ years[g,h]
	Central California[57]		Jan-Apr (Peak Mar-Apr)[b]								
Notoacmea scutum	Rockaway Beach, San Mateo County, CA[57]	I	Fall, winter, spring[b]								
Nucella canaliculata	San Juan Isl., WA[140]	I								2-3 years[c]	
	Tomales Bay, Marin County, CA[90]					Mar-May					
Nucella emarginata	San Juan Isl., WA[140]	I								1.5 years[c]	
	Bodega Bay, CA[90]					All year (Peak Nov-Feb)					
	Monterey Bay, CA[84]					Mar, Apr, June					
Petaloconchus montereyensis	Monterey, CA[71]	I	(Reproductive all year)								
Serpulorbis squamigerus	Southern California[71]	I	(Females ripe June-Aug+)								
	San Diego, CA[26]								Midsummer		
Tegula brunnea	Oregon[7]	I & S	Aug+[d]								
	Monterey, CA[84]		Mar+[d]								
Tegula funebralis	Oregon[50]	I									25 years[f]
	Oregon[51]		Summer[c]						(Peak Jan-Feb)		14-16 years[g]
	Central California[51]										6-8 years[g]
	Monterey Bay, CA[84]		Apr+[d]								
Mollusca Bivalvia (oysters, clams, mussels)											
Hinnites giganteus	Pacific Coast[13]	S									"Several decades"[c]
	Elkhorn Slough, Monterey County, CA[97]		Apr+[c]								

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Bivalvia (continued)											
Lithophaga plumula	Elkhorn Slough, Monterey County, CA[97]	I	Jan-Feb[c]					Length: 10 days			
	Newport Bay, Orange County, CA[99]		Jan+[c]								
Mytilus californianus	San Francisco, CA[141]	I & S	(Peak Aug & Jan)[c]								
	San Francisco, CA[120,153,154]		All year (Peak Oct-Nov, subpeaks Jan-Feb & May-June)[c]								
	Santa Barbara, CA[73]										≥8 years[f]
	Newport Bay, Orange County, CA[99]		May-June & Nov-Dec[c]								
	La Jolla, CA[155]		All year (Peak Oct-Mar)[d]								
	La Jolla, CA[156]								1-3 months after spawning		
Mytilus edulis	Oakland, CA[68]	I & S	Spring[c]						Mar-May		
	Elkhorn Slough, Monterey County, CA[97]		Spring-fall[c]								
	Monterey Bay, CA[139]										≥20 months[f]
	Morro Bay, CA[89]		Winter-spring[a]								
	Santa Barbara, CA[73]										2-6 years[f]
	Alamitos Bay, Long Beach, CA[110]		Fall-winter[b]						Winter-spring		
	Newport Bay, Orange County, CA[99]		Nov+[c]								
	La Jolla, CA[26]								Spring+		
Echinodermata Echinoidea (sand dollars, sea urchins)											
Strongylocentrotus franciscanus	Monterey Bay, CA[99]	I & S	Feb-Mar[c]								
	Monterey, CA[8]		Apr-May[a]								

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Echinodermata - Echinoidea (continued)											
Strongylocentrotus franciscanus (continued)	Corona del Mar, Orange County, CA[99]		Dec-Jan[c]								
	Southern California & Baja California[126]		Spring to early summer[+b]								
Strongylocentrotus purpuratus	Oregon[38]	I									≥10 years[f,h]
	Oregon[65,66]		Dec-May (Peak Dec-Mar)[c]							2 years[c]	
	Monterey Bay, CA[8,60,84,99]		Dec-May[a,c]								
	Southern California, & Baja California[126]		Spring-summer[b]								
Echinodermata Asteroidea (starfish)											
Leptasterias hexactis	San Juan Isl., WA[20]	I			Nov-Apr Length: 2 months						
	San Juan Isl., WA[105,106]				(Peak Mar)					2 years[c]	10 years[c]
	Monterey Bay, CA[83,84,99]				Feb-May[+]						
Leptasterias pusilla	Monterey, CA[138]	I			Jan-Apr Length: 17-19 days					1-2 years[c]	≥2 years[c]
Patiria miniata	Monterey Bay, CA[43,99]	I	Most or all year (Peak June-Aug)[a,c]								
	Corona del Mar, Orange County, CA[99]		Jan-July[c]								
Pisaster giganteus	Monterey Bay, CA[43,60]	I & S	Jan-Mar[a]								
Pisaster ochraceus	Pacific Coast[13]	I						Length: 6 weeks			
	San Juan Isl., WA[104,105]		June-Aug (Peak June)[a,b]					June-Aug Length: 2 months			
	San Juan Isl., WA[106]									5 years[c]	34 years[c]
	Monterey, CA[43,60,69,84]		Mar-June[a,d]								

Table II. Information on the life histories of Pacific coast benthic marine invertebrates associated with rocky substrata (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Chordata											
Ascidiacea (sea squirts)											
Styela montereyensis	Del Mar, Near San Diego, CA[131]	S							Summer		≤30 months[c]

LEGEND

Criteria used to determine spawning seasons, ages at sexual maturity, or maximum life expectancies:

a = gonad index
b = gamete ripeness or gonad turgidity
c = field observations
d = laboratory observations with or without artificial inducement
e = thickness of the gonad
f = growth rates
g = "annual" growth lines
h = size class data
i = animals maintained in aquaria

Other symbols:

+ = the author indicated that this event may also occur during other months of the year
I = intertidal
S = subtidal
Numbers identify the references

Table III. Information on the life histories of Pacific coast benthic marine invertebrates occurring in sand or mud habitats.

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Echiura (unsegmented worms)											
Urechis caupo	Pacific Coast[98,99,130]	S	Spring or early summer[c]					Length: ≤40 days			≥25 years[c]
Arthropoda Crustacea (lobsters, crabs, shrimps, barnacles)											
Callianassa californiensis	Pacific Coast[55,97,130]	I			All year (Peak June-July)						10-16 years[c]
Cancer gracilis	Elkhorn Slough, Monterey County, CA[97]	I & S		Nov	July-Aug						
Cancer magister	British Columbia, Canada[103]	S		Apr-Sep	Oct-Aug			Dec-Sept	(Peak Aug)	3-6 years[c]	8-10 years[c]
	Washington[24]			Feb-Dec (Peak May-June)	Nov-Feb			Jan-June	June-Aug[+]	2 years[c]	
	Oregon[148]				Oct-Mar			Apr-July			
	California[55,81,119]			Spring	Late fall-early winter			Winter Length: 3-5 months	May[+]	1.5-2 years[c]	6 years[c]
	Eureka-Crescent City, CA[37]				Jan-Feb[+]						
	San Francisco, CA[37]				Jan[+]					≤3 years[c]	
	San Francisco, CA[122]										7 years[f]
	San Francisco, CA[77]				All year						
	Elkhorn Slough, Monterey County, CA[97]			Mar							

Table III. Information on the life histories of Pacific coast benthic marine invertebrates occurring in sand or mud habitats (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Arthropoda - Crustacea (continued)											
Emerita analoga	Pacific Coast[99,154]	I		Summer or spring	Length: 4-5 months						
	Coos Bay, OR[42]				Aug+						
	California[42]				All year						
	Monterey, CA[12,60]				Apr-Aug						
	Southern California[55,130]			Spring-summer				Length: 4 months	(Peak May-July)	1 year[c]	2 years[c]
	Santa Barbara, CA[42]								Winter & spring		
	Santa Barbara area, CA[144]				June+			June+			
	Santa Monica, CA[41,42]									Males at 2 months, then become females at 14 months[c]	
	La Jolla, CA[40,42]					Summer		Length: 4.5 months	Apr-Aug (Peak May-July)		
	La Jolla, CA[31]				Feb-Sept					Males 2-3 months; females ≥6-8 months[c]	
Uca crenulata	Southern California[116]	I		June-Sept				Apr-Sept			
Mollusca Gastropoda (snails, limpets, abalones)											
Olivella biplicata	California[39]	I & S	(Reproductive all year)					Length: 10-28 days		1 year[c]	>10 years[c]
	San Diego, CA[142]									2-5 years[c,f]	8-12 years[c,f]
Mollusca Bivalvia (oysters, clams, mussels)											
Crassostrea gigas	California[6,36]	I	Spring & fall (Peak June-July)[c,d]								
Macoma nasuta	Elkhorn Slough, Monterey County, CA[97]	I & S	Summer[c]								

Table III. Information on the life histories of Pacific coast benthic marine invertebrates occurring in sand or mud habitats (continued).

Taxon	Geographic Location	l or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Bivalvia (continued)											
Ostrea lurida	Pacific Coast[55,130]	l			Length: 10-17 days			Length: 30-40 days		Males 5 months; females 6 months[c]	
	California[6]				Length: 10-14 days						
	Monterey Bay, CA[97]							Spring-summer			
	Newport Bay, CA[99]						July+[c]				
	La Jolla, CA[25,26,27,28]						Apr-Oct (Peak June-July)		Apr-Nov	4-6 months[c]	
Protothaca staminea	Pacific Coast[55,154]	l									7-10 years[g]
	British Columbia, Canada[52,53,130]		Jan-Mar[b,c]						Feb+	2-3 years[c]	8 years[c]
Saxidomus giganteus	British Columbia, Canada[52,54,55]	l & S	July-Sept[b]					Sept-Nov Length: 4 weeks		3-4 years[c]	17 years[g]
Saxidomus nuttalli	Pacific Coast[99]	I & S									10-15 years[c]
	Pacific Coast[55,154]		Spring-fall[c]								4-10 years[c]
Siliqua patula	Pacific Coast[81]	I & S								3-4 years[c]	
	Alaska[55,99,130,154]		July-Aug[c]								17 years[c]
	Washington[1,55,99,130,154]		May-June[c]								12 years[c]
	California[55,154]		Fall[c]					Length: 8 weeks		2 years[c]	6-8 years[c]
Tivela stultorum	Pacific Coast[1,45,46,55,99,154]	I & S	All year (Peak summer & fall)[c]					Length: "several weeks"		1-2 years[c]	26-35+ years[c]
	Pacific Coast[130]		Late summer[c]							2-3 years[c]	53 years[c]
	Pacific Coast[81]									3-4 years[c]	
	Central California[29]									2 years[c]	18-25 years[c]
	La Jolla, CA[29]									1-2 years[c]	10 years[c]
Tresus capax	Humboldt Bay, CA[101,102,151]	I & S	Winter[b,c]						Spring		20 years[f]

Table III. Information on the life histories of Pacific coast benthic marine invertebrates occurring in sand or mud habitats (continued).

Taxon	Geographic Location	I or S	Spawning Season	Mating Season	Brooding Period	Egg-Laying Period	Larval Release Period	Larval Period	Setting Period	Age at Sexual Maturity	Maximum Life Expectancy
Mollusca - Bivalvia (continued)											
Tresus nuttalli	Pacific Coast[55]	I & S	Spring-fall[c]							2 years[c]	
	Pacific Coast[81]									3-4 years[c]	
	Pacific Coast[154]		Winter-early spring[c]								
	Elkhorn Slough, Monterey County, CA[22,99]		All year (Peak Feb-Apr)[c]					Length: 21-30 days	All year (Peak Apr-May)	≥2 years[c]	≥17 years[c]
Zirfaea pilsbryi	Pacific Coast[99,130]	I & S	July+[c]								7-8 years[c]
Echinodermata Echinodea (sand dollars, sea urchins)											
Dendraster excentricus	Monterey Bay, CA[97]	I & S	July-Aug+[c]								
	San Diego area, CA[115]		Early spring-midsummer (Peak spring)[a]								

LEGEND

Criteria used to determine spawning seasons, ages at sexual maturity, or maximum life expectancies:

a = gonad index
b = gamete ripeness or gonad turgidity
c = field observations
d = laboratory observations with or without artificial inducement
e = thickness of the gonad
f = growth rates
g = "annual" growth lines
h = size class data
i = animals maintained in aquaria

Other symbols:

+ = the author indicated that this event may also occur during other months of the year
I = intertidal
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Numbers identify the references

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